

University of Groningen

## **Weather conditions affect levels of extra-pair paternity in the reed bunting *Emberiza schoeniclus***

Bouwman, KM; Komdeur, J

*Published in:*  
Journal of Avian Biology

*DOI:*  
[10.1111/j.2006.0908-8857.03611.x](https://doi.org/10.1111/j.2006.0908-8857.03611.x)

**IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.**

*Document Version*  
Publisher's PDF, also known as Version of record

*Publication date:*  
2006

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Bouwman, KM., & Komdeur, J. (2006). Weather conditions affect levels of extra-pair paternity in the reed bunting *Emberiza schoeniclus*. *Journal of Avian Biology*, 37(3), 238-244.  
<https://doi.org/10.1111/j.2006.0908-8857.03611.x>

### **Copyright**

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

### **Take-down policy**

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

## Weather conditions affect levels of extra-pair paternity in the reed bunting *Emberiza schoeniclus*

Karen M. Bouwman and Jan Komdeur

Bouwman, K. M. and Komdeur, J. 2006. Weather conditions affect levels of extra-pair paternity in the reed bunting *Emberiza schoeniclus*. – J. Avian Biol. 37: 238–244.

Extra-pair paternity (EPP) is common in many socially monogamous birds, but large variations in frequency of EPP are found both between and within species. Local ecological factors can affect the costs and benefits of extra-pair mating behaviour, and may therefore influence the chance that individuals engage in extra-pair copulations (EPCs). We investigated the effect of weather conditions during the peak fertile period of the female on the levels of EPP in reed buntings *Emberiza schoeniclus*. The reed bunting is a socially monogamous passerine, with extremely high levels of EPP (50% of offspring in 80% of broods). We found that higher daily minimum temperatures and more rainfall during the peak fertile period were associated with lower proportions of EPP. As during adverse weather conditions individuals have to invest more in self maintenance, we suggest that during long periods of rain the extra-pair mating behaviour of all individuals will be restricted, leading to lower proportions of EPP. During cold mornings, time-consuming activities such as mate guarding are likely to be more strongly affected than less time-consuming activities such as EPCs, leading to higher proportions of EPP.

K. M. Bouwman (correspondence) and J. Komdeur, Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands. E-mail: K.M.Bouwman@rug.nl

Extra-pair paternity (EPP) is common in many socially monogamous birds (Griffith et al. 2002), but large variations in frequency of EPP are found both between and within species (Petrie and Kempenaers 1998). Interspecies comparisons have found the occurrence of EPP to correlate with severable types of variables, such as adult mortality, level of paternal care, morphological characteristics and genetic variability (reviewed by Westneat and Stewart 2003). However, as levels of EPP can be highly variable not only between species, but also between populations of the same species (Gyllenstein et al. 1990, Bjornstad and Lifjeld 1997, Griffith et al. 1999) or even within a population between years (Langefors et al. 1998, Johnsen and Lifjeld 2003), it is essential to get a better understanding of factors influencing extra-pair mating behaviour on the individual level (Westneat and Stewart 2003). Local ecological factors can affect the costs and benefits of extra-pair mating behaviour (Birkhead and Møller 1992), and may

therefore influence the chance that individuals engage in extra-pair copulations (EPCs).

Adverse weather conditions may act as constraints on extra-pair mating behaviour through influencing energy expenditure or food availability and thus time budgets (Westneat 1994, Dawson and O'Connor 1996, Redpath et al. 2002, Vaclav et al. 2003). Up to date only one study investigated the effect of weather conditions (i.e. morning temperature and precipitation) on frequencies of EPP. In bluethroats *Luscinia s. svecica*, lower morning temperatures during the peak fertile period lead to lower levels of EPP in the brood, whereas the amount of precipitation had no effect (Johnsen and Lifjeld 2003). We investigated the effects daily minimum temperature and daily precipitation on levels of EPP in a population of reed buntings *Emberiza schoeniclus* in The Netherlands. The reed bunting is a socially monogamous passerine, with extremely high levels of EPP (50% of offspring in 80% of nests; Bouwman et al. 2005). When

adverse weather conditions (i.e. low minimum temperatures and high rainfall) were prevalent during the fertile period of the female, we expected a lower frequency of EPP in broods, because both males and females would have invested more effort in self-maintenance. Other variables that have been shown to explain variation in levels of EPP in reed buntings or other species, e.g. breeding density (Hoi and Hoi-Leitner 1997, Langefors et al. 1998, Richardson and Burke 2001; but see e.g. Sundberg and Dixon 1996, Tarof et al. 1998, Veiga and Boto 2000, Conrad et al. 2001) and age of the social parents (Bouwman and Komdeur 2005, Bouwman et al. 2006b; reviewed in Griffith et al. 2002), were included in the analyses.

## Methods

### Study area and data collection

From 2002 to 2003 we studied a population of reed buntings in a 13 ha study site, on the island of Noorderplaat (45 ha) in 'De Biesbosch' National Park in the Netherlands (51° 45'N, 4° 45'E). In 2002 and 2003 respectively 44 and 35 pairs were breeding within our study site. On average, 96% of adult reed buntings were caught using mist nets and ringed with a numbered aluminium ring and a specific combination of three colour rings for individual recognition. A blood sample was taken from the brachial vein for DNA analysis, and stored in 96% ethanol at room temperature.

Nests are built on or just above the ground and were located through systematic searches that flushed females off the nest, or by observing territorial birds for nest-related activities. The identities of the social pair of a nest were determined by direct or video observations of colour-ringed birds protecting the nest, incubating and feeding nestlings (for a description of the method using video recordings see Bouwman et al. 2005). Nestlings were blood sampled two days after hatching by taking a small blood sample from the leg vein. Unhatched eggs were inspected for embryonic development, which, if present, was used as a source of DNA. We located 97% of all nests that fledged young ( $n = 78$ ) in 2002 and 2003, and in only two cases did we see fledglings without first locating the nest.

### Fertile period

In general, females are expected to be fertile for the duration of sperm storage before the first egg is laid, until the day the penultimate egg is laid (Birkhead and Møller 1992). However, both mate guarding behaviour of male reed buntings (O'Malley 1993, Marthinsen et al. 2005) and intrusion rates by extra-pair males (O'Malley 1993) peak three days before the female lays the first egg

and dramatically drop after the first egg has been laid, indicating that this is likely to be the peak fertile period. A similar peak fertile period has been shown in other passerines (Krokene et al. 1996, Lifjeld et al. 1997, Sheldon and Ellegren 1998, Komdeur et al. 1999). Furthermore, weather conditions are more likely to change in a fertile period of nine days (i.e. five days before egg-laying until the day the penultimate egg is laid), than in a peak fertile period of four days, leading to less distinct patterns. We therefore defined the peak fertile period of a female as three days before the first egg was laid until the day the first egg was laid. As this methodology is consistent with that used by Johnsen and Lifjeld (2003), it allows a proper comparison between the two studies.

### Weather variables

Weather data were retrieved from the Royal Netherlands Meteorological Institute (KNMI) in De Bilt (The Netherlands), approximately 50 kilometers from our study site. Although the timing of EPCs in reed buntings is unknown, in many species both within- and extra-pair copulations occur mainly in the morning (Birkhead and Møller 1992, Double and Cockburn 2000, Johnsen and Lifjeld 2003). We expected low temperatures to have a larger impact on behaviour than high temperatures, and therefore retrieved daily minimum temperature ('Tmin') from the weather station. Furthermore, both the duration (in hours) and the amount (in mm) of precipitation is expected to impose constraints on the behaviour of individuals; thus these data were also retrieved. These three variables, i.e. the daily minimum temperature (°C), daily precipitation duration (hours) and daily precipitation (mm), were averaged over the days of peak fertility of the focal female. There were significant correlations between these variables among themselves and with the time of season (i.e. day the first egg of a clutch was laid (1 April = day 1); Table 1). To avoid potential problems concerning inter-correlated variables, we used a principle component analysis to create unrelated variables for certain weather conditions. This resulted in two principle components with eigen-values  $>1$ , which explained 93.8% of variance (Table 2). Principle component (PC)

Table 1. Correlations between weather variables and the first egg date of reed buntings nests ( $n = 121$ ) for the years 2002 and 2003 combined. The correlation coefficients are shown for daily minimum temperature (Tmin) in °C, daily amount of rainfall in mm and daily duration of rain in hours. The statistical significance is indicated by §:  $P < 0.1$ , \*:  $P < 0.05$  and \*\*\*:  $P < 0.001$ .

	First egg date	Tmin	Rainfall
Tmin (°C)	0.75***	–	
Rainfall (mm)	0.05	0.03	–
Rain duration (h)	–0.16§	–0.21*	0.78***

Table 2. Rotated component matrix including the variables minimum temperature ('Tmin'), rain duration (in h), and rainfall (in mm), following an extraction using principle component analysis.

Variables	PC1 'rain'	PC2 'temperature'
Tmin	-0.04	0.99
Rain duration	0.93	-0.20
Rainfall	0.95	0.10

1 strongly depended on the two variables describing rainfall, while PC2 strongly depended on the daily minimum temperature (Table 2). Therefore, PC1 and PC2 were called 'rain' and 'temperature', respectively.

### Other variables

Because more than 90% of all extra-pair sires were resident within two territories of the focal female (Bouwman et al. 2006a), we determined breeding density at a local scale. Local breeding density was defined as the number of territories that were at least partly located within a 100 m radius (i.e. approximate equivalent of including two territories) around the focal nest.

We were unable to reliably determine the age of males and females based on plumage characteristics. However, we previously showed that wing length increases significantly from one year to the next ( $P < 0.001$ , Bouwman et al. 2006b). We therefore included wing length as measure for male and female age.

### Paternity analysis

DNA was extracted from blood samples using salt extraction (Richardson et al. 2001). Individuals were genotyped using six fluorescently labelled microsatellite markers: Escu1, Escu4, Escu6 (Hanotte et al. 1994), Pdoj5 (Griffith et al. 1999), Mcyu4 (Double et al. 1997) and Ppi2 (Martinez et al. 1999). Parentage was determined by using a likelihood-based approach in CERVUS (version 2.0; Marshall et al. 1998). This program assesses the confidence of paternity exclusion using criteria generated through a simulation taking into account allele frequencies in the population, the number of possible candidate parents, the proportion of candidate parents sampled, and the percentage of missing genetic data and genotyping errors. CERVUS was given the choice between two candidate parents: the social male and one potential, but unknown, extra-pair male. The program calculates the likelihood that the social male is the actual father by using the natural logarithm of the likelihood ratio or so called LOD score. The social male is assigned as the father if the LOD-score is positive and rejected if the LOD-score is zero or below. To accept the male as the father, a critical difference is required in

LOD scores between the first and the second candidate. The critical values were calculated by entering the following simulation parameters in CERVUS: 2 candidate parents and 50% of candidate parents sampled. Assigned males were accepted at  $>95\%$  confidence; a maximum of one mismatch was allowed. None of the loci deviated significantly from Hardy-Weinberg equilibrium. Using the observed allele frequencies, CERVUS calculated a total exclusionary power for the six microsatellite loci; in both years the probability of exclusion was 0.993 for assigning the father when the mother is unknown ('first parent') and 0.999 for assigning the father when the mother is known ('second parent').

In 2002 and 2003 combined, 501 offspring were genotyped from 129 nests. For 473 offspring the social male was known. The genotype of the social male showed no mismatch with the genotype of the offspring in 40% of the cases ( $n = 473$ ), one mismatch in 9% of the cases, and more than one mismatch in 51% of the cases. Extra-pair males thus sired 54.6% of offspring in 2002 ( $n = 262$ ) and 46.4% of offspring in 2003 ( $n = 211$ ).

### Data analyses

We used multilevel generalised linear models to analyse the effect of weather conditions on the proportion of EPP in a brood, assuming a binomial error distribution with logit-link function and using the number of offspring in the brood as the denominator. The two-level hierarchical structure of the proportional response data (i.e. proportion of EPP in a brood) was built up with the identity of the pair as the highest level and the broods belonging to each pair as the lowest level. This approach allowed us to make full use of all available data, while at the same time accounting for (i) having included pairs more than once, as often a pair produced more than one brood in a season or in different years, and (ii) the number of offspring in a brood, which varied between two and five offspring. The model was implemented using reweighted iterative generalised least squares (RIGLS) and 2nd order penalised quasi-likelihood approximation (PQL; Rasbash et al. 2004). The significance of variables was tested using the Wald statistic, which follows a  $\chi^2$ -distribution. Variables with  $P > 0.1$  were backwards eliminated, starting with interaction terms. We present the Wald statistic values of the variables in the final model and of the eliminated variables prior to elimination. As females may actively chose not to engage in extra-pair copulations (Birkhead and Møller 1992), we also performed the multivariate analysis only using broods with at least one extra-pair offspring (following Johnsen and Lifjeld 2003).

Statistical analyses were performed using SPSS 11.0.1 (2001) and MLwiN 2.0. Means are expressed with

standard errors, probability values are two-tailed and we assumed significance if  $P < 0.05$ .

## Results

The average daily minimum temperature, rainfall and rain duration during peak fertile periods were not significantly different between the years (all  $P > 0.36$ ). Year, time of season, male and female wing length (as measures for age) did not significantly explain any additional variation in proportion of EPP (Table 3). We found a significant negative effect of PC1 'rain' (Table 3; Fig. 1a) and a tendency for a positive effect of local breeding density on the proportion of EPP (Table 3). When excluding broods that did not contain any extra-pair offspring from the analysis, PC2 'temperature' negatively predicted the proportion of EPP in her brood (Table 3, Fig. 1b). No effect of local breeding density was found in this analysis.

## Discussion

Daily minimum temperature and rainfall during the peak fertile period of the female both had a negative effect on the proportion of EPP in her brood; the first when including nests containing EPP and the latter when including all nests. Although there is a positive correlation between minimum temperature and first egg date, the association between minimum temperature and EPP could not be explained by the time of season at which the clutch was produced. Minimum temperatures are likely to affect the amount of time that individuals have to invest in self-maintenance (Dawson and O'Connor 1996). In addition, insect abundance will decrease with lower temperatures (Pollard et al. 1996), making foraging more difficult. As in the study on bluethroats, minimum temperatures were only found to significantly affect levels of EPP when only including nests with EPP.

However, in contrast to the results found in bluethroats (Johnsen and Lifjeld 2003), lower minimum temperatures during the fertile period lead to higher proportions of EPP. For bluethroats in Norway, weather conditions encountered especially early in the breeding season will be much harsher (e.g. reports of snow; Johnsen and Lifjeld 2003) than for reed buntings in the Netherlands. Therefore the trade-off between self-maintenance and extra-pair mating behaviour is expected to be stronger in Norway, leading to the negative relationship between morning temperature and EPP (Johnsen and Lifjeld 2003). Possibly energy demands during low temperatures in the Netherlands are such that time-consuming activities, such as mate guarding, are limited, but less time-consuming activities, such as EPCs (Dickinson 1997), are not. Reed buntings forage mainly off their territory on communal feeding grounds (Cramp and Perrins 1994, pers. obs.), which is likely to conflict with other behaviours such as mate guarding (Westneat 1994, Komdeur 2001). Although mate guarding behaviour has not been studied in our population, in Norwegian reed buntings mate guarding has been found to be effective in protecting paternity (Marthinsen et al. 2005). We therefore suggest that at low temperatures, mate guarding is traded against self-maintenance, e.g. foraging, thereby increasing the opportunity for females and extra-pair males to gain EPCs. At higher minimum temperatures, mate guarding behaviour may be less constrained, resulting in lower levels of EPP.

In serins *Serinus serinus*, levels of EPP were higher in territories with high food availability (Hoi-Leitner et al. 1999). The authors suggest that this relation is a result of females in good quality habitat being less dependent on male assistance in caring for offspring and therefore being more likely to seek EPCs (Hoi-Leitner et al. 1999). However, Johnsen and Lifjeld (2003) prefer the interpretation that in serins, as in bluethroats, extra-pair behaviour is constrained by energy demands. In contrast to the study on serins, but in agreement with our study, lower levels of EPP were found in broods of

Table 3. Multilevel generalised linear model of the relation between PC1 'rain' and PC2 'temperature' during the peak fertile period of the female and the proportion of EPP in reed bunting nests for the years 2002 and 2003. Other variables which potentially influence the proportion of EPP (i.e. year, time of season ('first egg date'), wing length of the male and female (as measures for age) and local breeding density) are initially included in the multivariate analysis; wherein (i) all broods are included ( $n = 121$ ), and (ii) only broods containing EPP are included ( $n = 88$ ). The direction of the parameter estimates, values of the Wald test statistics and their significance (prior to removal from the model) are shown. The values of variables included in the final model are highlighted in bold.

Variable	All broods		Broods containing EPP	
	Wald	P	Wald	P
Year	-0.83	0.36	+0.14	0.71
First egg date	-0.09	0.76	+0.02	0.89
Wing length male	-1.83	0.18	-1.17	0.28
Wing length female	+1.36	0.24	+2.25	0.13
Density	+3.23	0.072	+0.64	0.42
PC1 'rain'	-4.32	0.038	-1.09	0.30
PC2 'temperature'	-1.27	0.26	-4.09	0.043

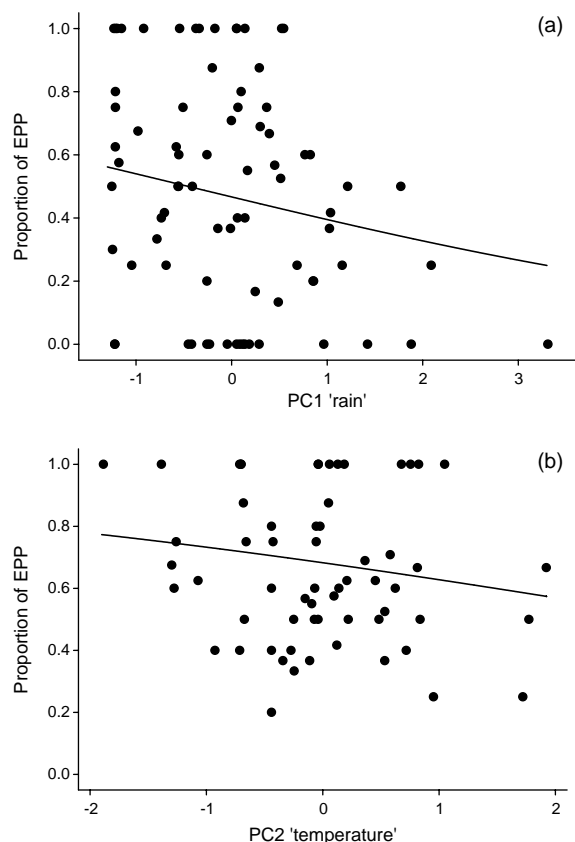


Fig. 1. Relationship between the proportion of EPP in a brood and (a) PC1 'rain', while including all broods ( $n=121$ ), and (b) PC2 'temperature', while only including broods containing at least one extra-pair offspring ( $n=88$ ), during the peak fertile period of the female in reed buntings for the years 2002 and 2003. As the data were analysed using a multilevel GLM with pair identity on the highest level, the data in the figure are presented as the average proportion of EPP per pair; (a)  $n=79$ , (b)  $n=62$ . The line represents the predicted values of the final model.

food-supplemented red-winged blackbirds *Agelaius phoeniceus* (Westneat 1994). The time budget of especially the male red-winged blackbird was affected by the availability of additional food: with extra food, males spent more time on their territories. As EPCs only occurred on the female's territory, the increased presence of the social male on the territory allowed him to prevent more EPCs (Westneat 1994). Similarly, in house sparrow broods *Passer domesticus* levels of EPP were lower when the social parents were food-supplemented (Vaclav et al. 2003). However, in this species, females, but not males, spent more time at the nest when extra food was available. This resulted in partners being together for a longer period of time and consequently lower levels of EPP in the brood (Vaclav et al. 2003).

More rainfall during the peak fertile period of reed buntings lead to a lower proportion of EPP in the brood, but only when including all broods. During rain, all

individuals probably seek cover to avoid getting wet, and thus avoid an increase in energy expenditure (Nye 1964, McCafferty et al. 1997). Furthermore, foraging is likely to be more difficult, as insects are less active and thus less easy to find during rain (Poulsen 1996, Pollard et al. 1996). Therefore, as during low temperatures, mate guarding is likely to be relaxed. However, the costs for the female to seek EPCs during rainfall are presumably higher (i.e. getting wet resulting in increased energy expenditure) than during low temperatures, thus restricting movements of all individuals and not only those of the social male. The effect of the amount of rainfall was not as strong as the effect of the duration of rainfall; longer periods of rain is more restrictive to the behaviour of individuals than lots of rain which may fall in a relatively short period of time. The study on bluethroats showed that levels of EPP were not affected by the amount of rain (Johnsen and Lifjeld 2003), however, the duration of rainfall was not included in the analysis. Long-lasting rain may impose larger constraints on behaviour than a short, heavy rain shower.

When including all nests in the analysis, the proportion of EPP in broods tended to increase with higher local breeding densities, but no effect of breeding density was found when excluding nests without EPP. At higher breeding densities, searching costs for extra-pair mates may be reduced (Westneat 1990, Birkhead and Møller 1992). However, greater densities may also impose costs, as the number of territorial intrusions by potential extra-pair males increase (Komdeur et al. 1999), thereby increasing the chance of losing paternity in a male's own nest (Birkhead and Møller 1992). In addition, females may experience more harassment by extra-pair males (Morton et al. 1990). A positive relationship was found in several studies (Hoi and Hoi-Leitner 1997, Langefors et al. 1998, Richardson and Burke 2001), while others failed to find a relationship (Dunn et al. 1994, Sundberg and Dixon 1996, Tarof et al. 1998, Veiga and Boto 2000, Conrad et al. 2001). Possibly the breeding density in our population exceeded a certain threshold level, resulting in sufficient extra-pair mating partners available at all densities throughout the study site (Dunn et al. 1994, Tarof et al. 1998). Alternatively, mate guarding behaviour may increase as a response to a higher cuckoldry risk with increasing density (Dickinson and Leonard 1996, Komdeur 2001, but see Vaclav and Hoi 2002), resulting in similar levels of EPP in nests at low and high densities. Unfortunately, we do not know whether mate guarding in the reed bunting is affected by breeding densities.

## Concluding remarks

Our data show that weather conditions during the peak fertile period of female reed buntings affect levels of EPP.

This is in agreement with the results found in bluethroats (Johnsen and Lifjeld 2003), although mechanisms seem to differ between these species. As weather conditions may explain part of the variation found in EPP within and between species, they deserve more attention from researchers studying EPP. Our next step would be to determine the specific role played by male and female reed buntings in extra-pair mating, and which aspects are affected by ecological factors. Detailed behavioural observations are required to answer these questions.

**Acknowledgements** – We thank Jan Wijmenga, René van Dijk, Cas Eikenaar, Suzette Flantua and Leonie Raijmakers for their assistance in the field. Staatsbosbeheer kindly allowed us to work and live in “De Biesbosch”, and we are especially grateful to Dirk Feij and Bart Weel who arranged the practicalities. Martijn van de Pol provided valuable statistical advice. This manuscript benefited from constructive comments from Rudi Drent, Cas Eikenaar, Dave Westneat and Jan Lifjeld. Financial support was provided by NWO to JK (809-34-005) and Schure-Beijerinck-Popping Fund of KNAW to KMB (SBP/JK/2003-30).

## References

- Birkhead, T. R. and Møller, A. P. 1992. Sperm competition in birds. Evolutionary causes and consequences. – Academic Press, London.
- Bjornstad, G. and Lifjeld, J. T. 1997. High frequency of extra-pair paternity in a dense and synchronous population of willow warblers *Phylloscopus trochilus*. – J. Avian Biol. 28: 319–324.
- Bouwman, K. M. and Komdeur, J. 2005. Old female reed buntings (*Emberiza schoeniclus*) increase extra-pair paternity in their broods when mated to young males. – Behaviour 142: 1449–1463.
- Bouwman, K. M., Lessells, C. M. and Komdeur, J. 2005. Male reed buntings do not adjust parental effort in relation to extra-pair paternity. – Behav. Ecol. 16: 499–506.
- Bouwman, K. M., Burke, T. and Komdeur, J. 2006a. How reed buntings benefit from extra-pair mating behaviour: testing hypotheses through patterns of paternity in sequential broods. – Mol. Ecol.: In press.
- Bouwman, K. M., Van Dijk, R. E., Wijmenga, J. J. and Komdeur, J. 2006b. Older male reed buntings are more successful at gaining extra-pair fertilisations. – Anim. Behav.: In press.
- Conrad, K. F., Johnston, P. V., Crossman, C., Kempenaers, B., Robertson, R. J., Wheelwright, N. T. and Boag, T. 2001. High levels of extra-pair paternity in an isolated, low-density, island population of tree swallows (*Tachycineta bicolor*). – Mol. Ecol. 10: 1301–1308.
- Cramp, S. and Perrins, C. M. 1994. The birds of the western Palearctic, Vol. IX: buntings and New World warblers. – Oxford University Press, Oxford.
- Dawson, W. R. and O'Connor, T. P. 1996. Energetic features of avian thermoregulatory responses. – In: Carey, C. (ed.). Avian energetics and nutritional ecology. Chapman & Hall, New York, pp. 85–124.
- Dickinson, J. L. 1997. Male detention affects extra-pair copulation frequency and pair behaviour in western bluebirds. – Anim. Behav. 53: 561–571.
- Dickinson, J. L. and Leonard, M. L. 1996. Mate attendance and copulatory behaviour in western bluebirds: Evidence of mate guarding. – Anim. Behav. 52: 981–992.
- Double, M. and Cockburn, A. 2000. Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. – Proc. R. Soc. B 267: 465–470.
- Double, M. C., Dawson, D., Burke, T. and Cockburn, A. 1997. Finding the fathers in the least faithful bird: A microsatellite-based genotyping system for the superb fairy-wren *Malurus cyaneus*. – Mol. Ecol. 6: 691–693.
- Dunn, P. O., Whittingham, L. A., Lifjeld, J. T., Robertson, R. J. and Boag, P. T. 1994. Effects of breeding density, synchrony, and experience on extra-pair paternity in tree swallows. – Behav. Ecol. 57: 1071–1081.
- Griffith, S. C., Owens, I. P. F. and Thuman, K. A. 2002. Extra-pair paternity in birds: a review of interspecific variation and adaptive function. – Mol. Ecol. 11: 2195–2212.
- Griffith, S. C., Stewart, I. R. K., Dawson, D. A., Owens, I. P. F. and Burke, T. 1999. Contrasting levels of extra-pair paternity in mainland and island populations of the house sparrow (*Passer domesticus*): is there an ‘island effect’? – Biol. J. Linn. Soc. Lond. 68: 303–316.
- Gyllenstein, U. B., Jakobsson, S. and Temrin, H. 1990. No evidence for illegitimate young in monogamous and polygynous warblers. – Nature 343: 168–170.
- Hanotte, O., Zanon, C., Pugh, A., Greig, C. and Dixon, A. 1994. Isolation and characterization of microsatellite loci in a passerine bird: the reed bunting *Emberiza schoeniclus*. – Mol. Ecol. 3: 529–530.
- Hoi, H. and Hoi-Leitner, M. 1997. An alternative route to coloniality in the bearded tit: females pursue extra-pair fertilizations. – Behav. Ecol. 8: 113–119.
- Hoi-Leitner, M., Hoi, H., Romero-Pujante, M. and Valera, F. 1999. Female extra-pair behaviour and environmental quality in the serin (*Serinus serinus*): a test of the ‘constrained female hypothesis’. – Proc. R. Soc. B 266: 1021–1026.
- Johnsen, A. and Lifjeld, J. T. 2003. Ecological constraints on extra-pair paternity in the bluethroat. – Oecologia 136: 476–483.
- Komdeur, J. 2001. Mate guarding in the Seychelles warbler is energetically costly and adjusted to paternity risk. – Proc. R. Soc. B 268: 2103–2111.
- Komdeur, J., Kraaijeveld-Smit, F., Kraaijeveld, K. and Edelaar, P. 1999. Explicit experimental evidence for the role of mate guarding in minimizing loss of paternity in the Seychelles warbler. – Proc. R. Soc. B 266: 2075–2081.
- Krokene, C., Anthonisen, K., Lifjeld, J. T. and Amundsen, T. 1996. Paternity and paternity assurance behaviour in the bluethroat, *Luscinia s. svecica*. – Anim. Behav. 52: 405–417.
- Lanfords, A., Hasselquist, D. and von Schantz, T. 1998. Extra-pair fertilizations in the sedge warbler. – J. Avian Biol. 29: 134–144.
- Lifjeld, J. T., Slagsvold, T. and Ellegren, H. 1997. Experimental mate switching in pied flycatchers: male copulatory access and fertilization success. – Anim. Behav. 53: 1225–1232.
- Marshall, T. C., Slate, J., Kruuk, L. E. B. and Pemberton, J. M. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. – Mol. Ecol. 7: 639–655.
- Marthinsen, G., Kleven, O., Brenna, E. and Lifjeld, J. T. 2005. Part-time mate guarding affects paternity in male reed buntings (*Emberiza schoeniclus*). – Ethology 111: 397–410.
- Martinez, J. G., Soler, J. J., Soler, M., Møller, A. P. and Burke, T. 1999. Comparative population structure and gene flow of a brood parasite, the great spotted cuckoo (*Clamator glandarius*), and its primary host, the magpie (*Pica pica*). – Evolution 53: 269–278.
- McCafferty, D. J., Moncrief, B. J. and Taylor, I. R. 1997. The effect of wind speed and wetting on thermal resistance of the barn owl (*Tyto alba*). I. Total heat loss, boundary layer and total resistance. – J. Therm. Biol. 22: 253–264.
- Morton, E. S., Forman, L. and Braun, M. 1990. Extrapair fertilizations and the evolution of colonial breeding in purple martins. – Auk 107: 275–283.
- Nye, P. 1964. Heat loss in wet ducklings and chicks. – Ibis 106: 189–197.

- O'Malley, S. L. C. 1993. Mating behaviour and reproductive success in the reed bunting *Emberiza schoeniclus*. – Ph.D. thesis, University of Leicester, Leicester.
- Petrie, M. and Kempenaers, B. 1998. Extra-pair paternity in birds: explaining variation between species and populations. – *Trends Ecol. Evol.* 13: 52–58.
- Pollard, R. H., Ballard, W. B., Noel, L. E. and Cronin, M. A. 1996. Parasitic insect abundance and microclimate of gravel pads and tundra within the Prudhoe Bay oil field, Alaska, in relation to use by caribou, *Rangifer tarandus granti*. – *Canadian Field-Naturalist* 110: 649–658.
- Poulsen, B. O. 1996. Relationships between frequency of mixed-species flocks, weather and insect activity in a montane cloud forest in Ecuador. – *Ibis* 138: 466–470.
- Rasbash, J., Steele, F., Browne, W. and Prosser, B. 2004. A user's guide to MLwiN-Version 2.0. – Centre for Multilevel Modelling, London.
- Redpath, S. M., Arroyo, B. E., Etheridge, B., Leckie, F., Bouwman, K. and Thirgood, S. J. 2002. Temperature and hen harrier productivity: from local mechanisms to geographical patterns. – *Ecography* 25: 533–540.
- Richardson, D. S. and Burke, T. 2001. Extrapair paternity and variance in reproductive success related to breeding density in Bullock's orioles. – *Anim. Behav.* 62: 519–525.
- Richardson, D. S., Jury, F. L., Blaakmeer, K., Komdeur, J. and Burke, T. 2001. Parentage assignment and extra-group paternity in a cooperative breeder: the Seychelles warbler (*Acrocephalus sechellensis*). – *Mol. Ecol.* 10: 2263–2273.
- Sheldon, B. C. and Ellegren, H. 1998. Paternal effort related to experimentally manipulated paternity of male collared flycatchers. – *Proc. R. Soc. B* 265: 1737–1742.
- Sundberg, J. and Dixon, A. 1996. Old, colourful male yellow-hammers, *Emberiza citrinella*, benefit from extra-pair copulations. – *Anim. Behav.* 52: 113–122.
- Tarof, S. A., Stutchbury, B. J. M., Piper, W. H. and Fleischer, R. C. 1998. Does breeding density covary with extra-pair fertilizations in hooded warblers? – *J. Avian Biol.* 29: 145–154.
- Vaclav, R. and Hoi, H. 2002. Importance of colony size and breeding synchrony on behaviour, reproductive success and paternity in house sparrows *Passer domesticus*. – *Folia Zoologica* 51: 35–48.
- Vaclav, R., Hoi, H. and Blomqvist, D. 2003. Food supplementation affects extrapair paternity in house sparrows (*Passer domesticus*). – *Behav. Ecol.* 14: 730–735.
- Veiga, J. P. and Boto, L. 2000. Low frequency of extra-pair fertilisations in house sparrows breeding at high density. – *J. Avian Biol.* 31: 237–244.
- Westneat, D. F. 1990. Genetic parentage in the indigo bunting: a study using DNA fingerprinting. – *Behav. Ecol. Sociobiol.* 27: 67–76.
- Westneat, D. F. 1994. To guard mates or go forage-conflicting demands affect the paternity of male red-winged blackbirds. – *Am. Nat.* 144: 343–354.
- Westneat, D. F. and Stewart, I. R. K. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. – *Ann. Rev. Ecol. Evol. Syst.* 34: 365–396.

(Received 3 January 2005, revised 5 April 2005, accepted 12 April 2005.)